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EVOLUTION AND SYSTEMATICS OF THE ONAGRACEAE: FLORAL ANATOMY¹

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ABSTRACT

Analysis of floral structure in all onagraceous genera—with *Lopezia* and *Ludwigia* studied most intensively—indicates that the earliest onagrads were isomerous and diplostemonous and had more than four appendages in each whorl. Deeply cleft placentas bore more or less 2-seriate ovules as in *Hauya* and some fuchsias. The ovary was superior within a floral cup that probably varied in prominence from species to species. The nectary was at the junction of cup and gynoecium as in some modern Lythraceae. These old onagrads gave rise to two lines. One line, surviving today as *Ludwigia*, specialized early for wet conditions and higher ovule number. The ovary became inferior with the (minimal?) floral cup disappearing *pari passu* and the nectaries migrating to the ovary's summit; there was no floral tube beyond the ovary and no link with a particular pollinator. A double-barreled vascular supply evolved along with *Ludwigia*'s massive placentas. In the main onagraceous line the inferior ovary evolved independently and without a dual supply. Eventually coevolution with long-tongued pollinators changed the floral cup to an epigynous tube with nectariferous tissue on the tube side of the tube-gynoecium junction. The tube was then lost in certain derivatives of the main onagraceous line: *Gayophytum*, *Gongylocarpus*, *Lopezia*, *Epilobium* sect. *Chamaenerion*, and some circaeas. Some features of onagraceous flowers merit our attention because they may illuminate problems of floral evolution in families unrelated to the Onagraceae. One such feature is the commissural stigma of *Clarkia* and *Epilobium*. *Gayophytum*'s gynoecial vasculature is another.

I first looked into onagraceous flowers because I wanted to understand a peculiarity—transseptal ovular bundles—in an unrelated group (Eyde, 1967). I had learned from the striking diagrams of Baehni and Bonner (1948; Bonner, 1948) that many of the onagrads also supply their ovules via the transseptal route rather than the familiar central route, and I thought there might be transitional forms in the family to aid in explaining this. That is, I hoped that some of the onagrads would turn out to be intermediate for the trait and that the intermediates would show something about the evolution of transseptal vasculature from an ancestral central system.

In time, I learned Baehni and Bonner had not been the first to find transseptal

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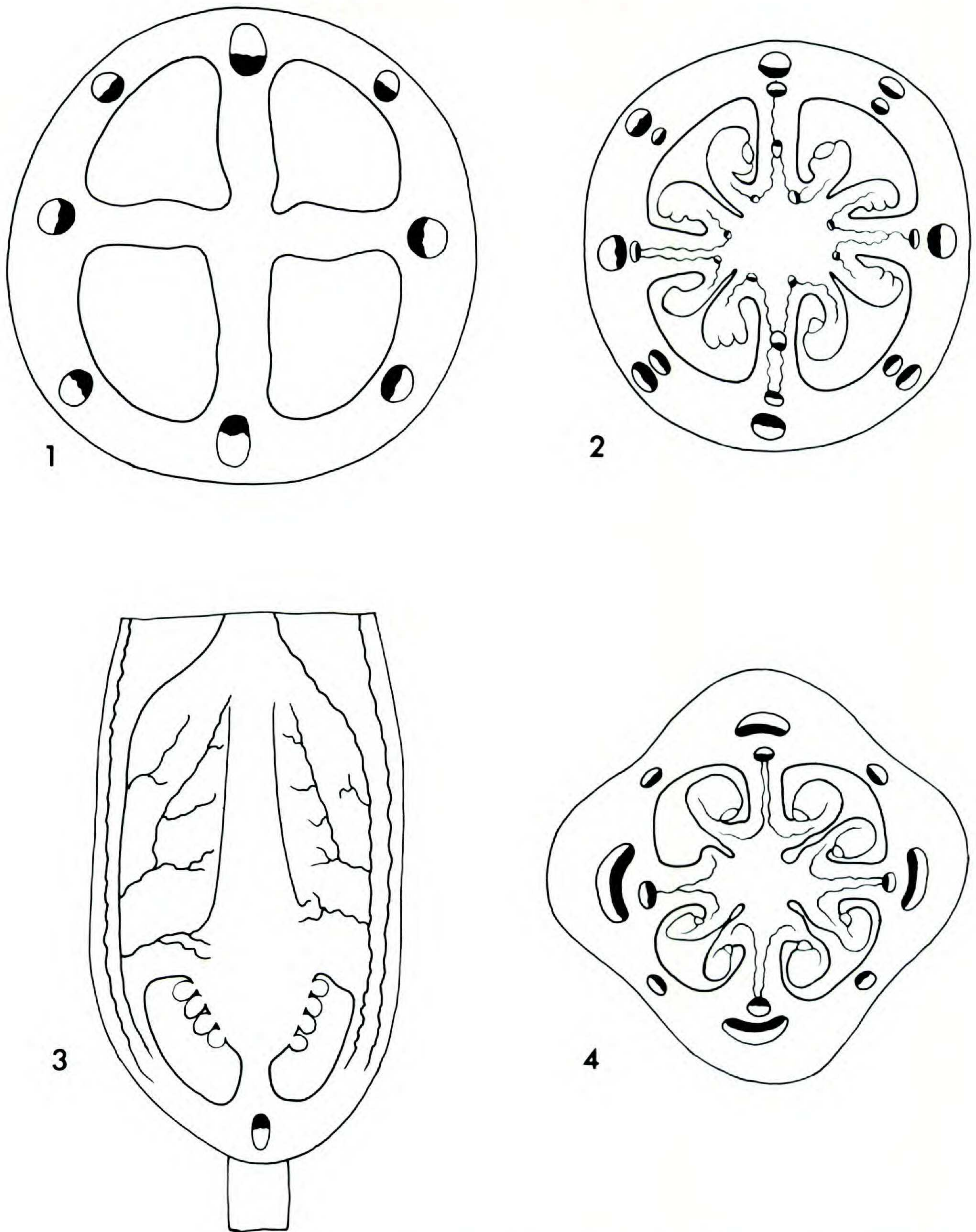
bundles in the Onagraceae. Indeed, Van Tieghem (1868, 1875) illustrated the trait in his prize-winning work on gynoecial vasculature (Figs. 1–4). I learned, too, that although the trait occurs in every genus of the Onagraceae, no genus shows the transition I had envisioned, a central supply going over to a transseptal supply. *Ludwigia* does have a dual system, central and transseptal, in almost every species, but there are several lines of evidence to mark *Ludwigia* as an early offshoot with traits of its own rather than a repository of transitional traits (Eyde, 1981).

Ludwigia's special features include the massive, highly ovuliferous placentas found in species that are on other grounds closest to *Ludwigia*'s ancestry. Another noteworthy feature is the lack of a floral tube beyond the ovary. Ludwigiads are not the only tubeless onagrads, to be sure, but they are the only tubeless onagrads without a constriction or neck between the inferior ovary and the epigynous part of the flower. The oddest trait of all is the way *Ludwigia*'s nectaries are placed. The more archaic ludwigiads have four or five or more depressed, hair-fringed nectaries—the number depends on the flower's merism—on the raised roof of each ovary, where they occupy the same radii as the ovary's locules. In other onagraceous genera the nectary is commonly a continuous circular region at the junction of the floral tube and the gynoecium. Or, if the nectary extends above that junction, it is clearly on the junction's androecial side rather than its gynoecial side.

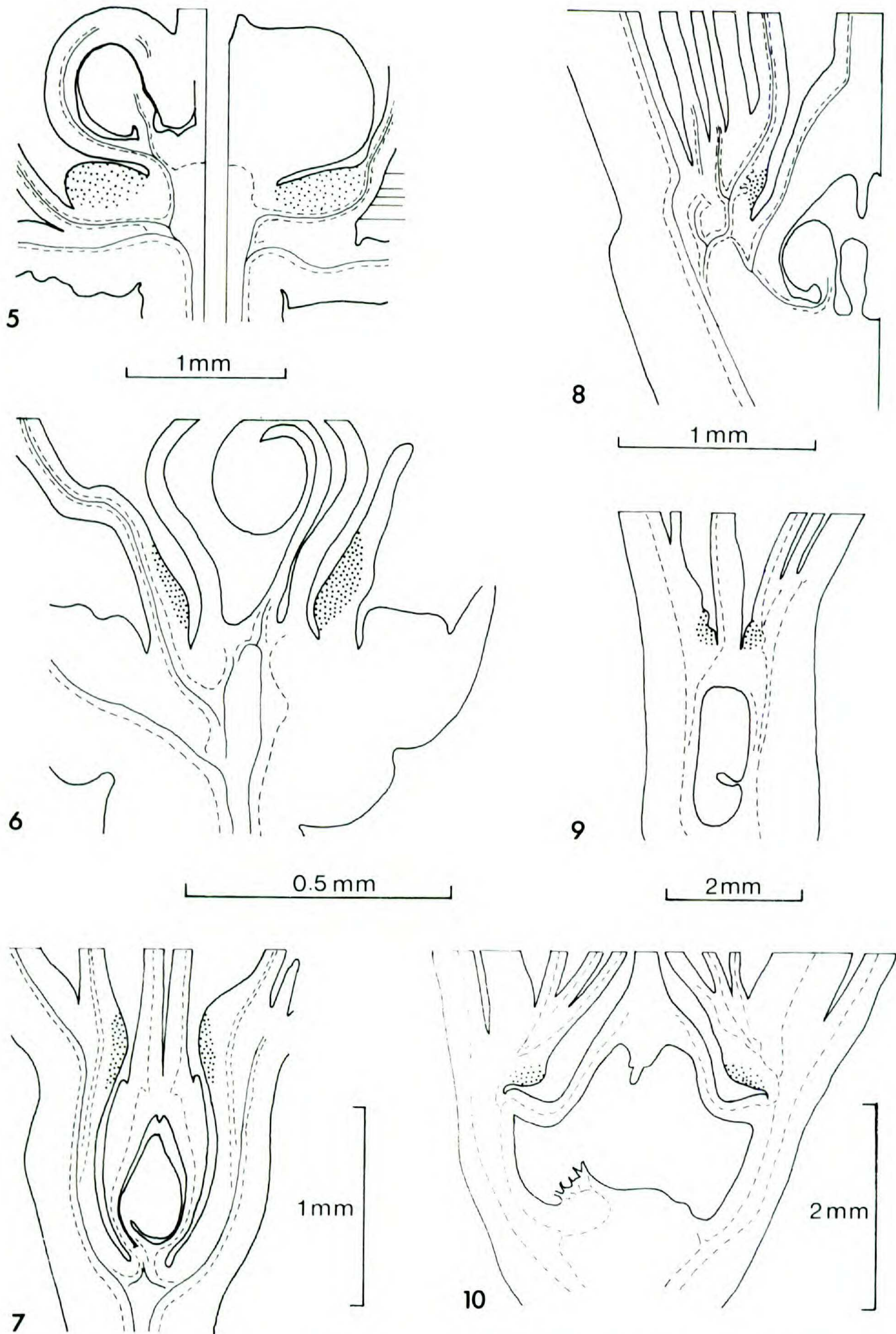
I once tried to use nectary position to link *Ludwigia* with *Lopezia* because flowers of both genera, when cross-sectioned, can show nectariferous tissue alternating with the androecial appendages. *Lopezia*'s nectaries, however, are definitely on the androecial side of the gynoecium-androecium junction. Some sections even show secretory tissue in the base of the single stamen and in that of the accompanying staminode (Eyde & Morgan, 1973: figs. 2f & 6f).

Looking into the literature on nectaries for a model—for a group in which interstaminal nectaries seem to have moved from the gynoecial side of the junction to the androecial side or vice versa—I found none. On the contrary, there are a number of groups in which the nectary's position is constant with respect to the junction. The Caryophyllales are the outstanding example. Zandonella's (1972, 1977) examination of 400 species in this order's 11 families turned up no gynoecial nectaries. All caryophyllalean nectaries are on the androecial side of the junction (Figs. 5–10) except in the Phytolaccaceae, thought to be the archaic family, where the nectary can be at the junction without extending more to one side than the other. The Rosaceae are another group in which the nectary is never on the gynoecium. The rosaceous nectary is part of the floral cup, and apparently it is the evolutionary reason for the floral cup: the cup is an expanded nectariferous surface shaped to hold the nectar for pollinators. Brown (1938: 558) may have been the first to apprehend that. A contrasting list of families with nectaries on the gynoecial side of the junction (some members having them at the junction) would include Acanthaceae, Crassulaceae, Ericaceae, Gesneriaceae, and Scrophulariaceae. Figures 11–14 show flowers with gynoecial nectaries.

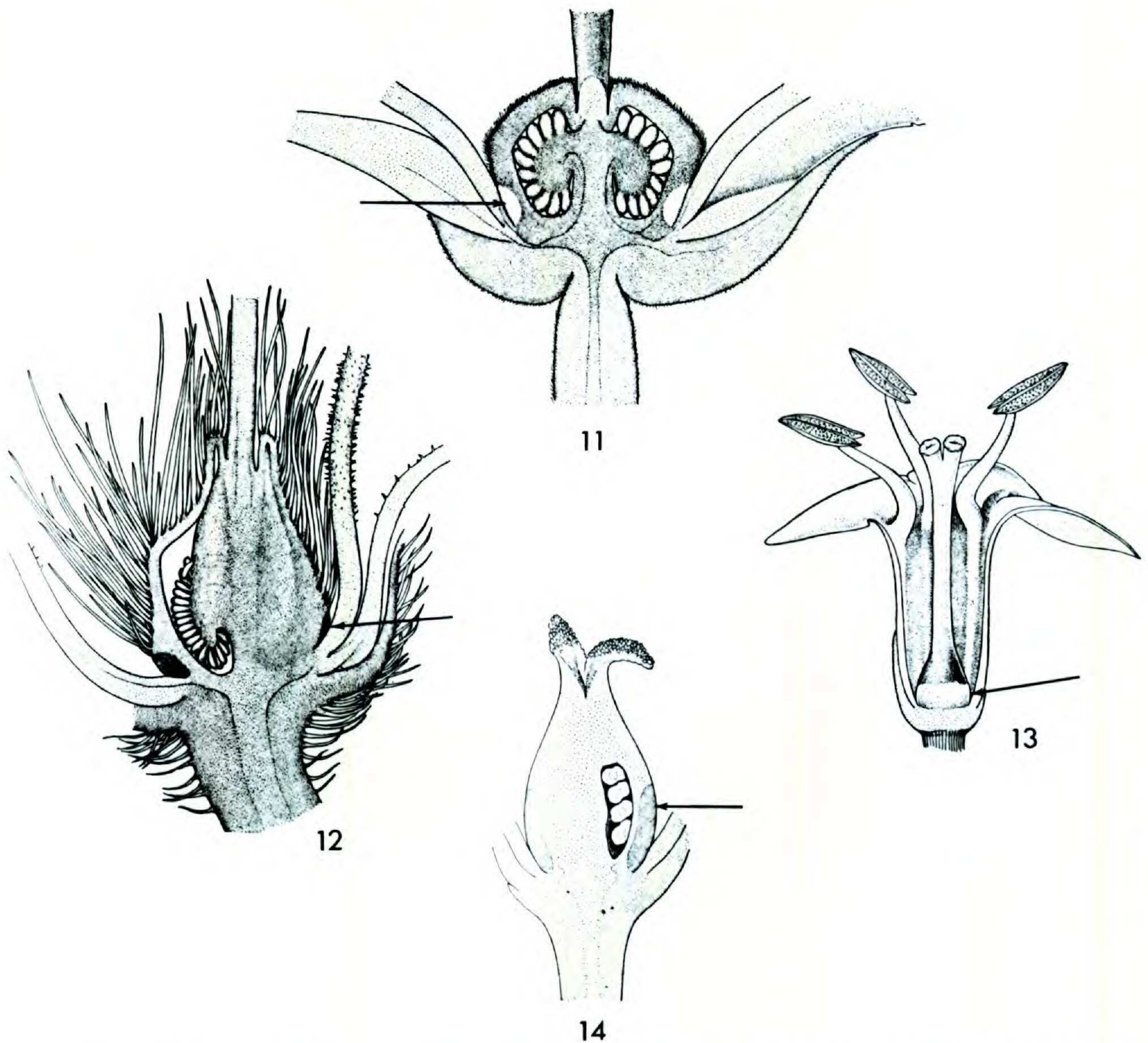
The explanation for all this, I think, is that many floral nectaries began phylogenetically at the junction of the gynoecium and surrounding parts, where mechanical stress could trigger cell divisions (see Lintilhac, 1974; Lintilhac & Vesecky, 1980, on stress and morphogenesis). Selection for increased secretion could then



FIGURES 1-4. Four of Van Tieghem's (1875) 13 diagrams of floral vasculature in Onagraceae, redrawn with minor transverse bundles of (inferior) ovary wall left out.—1-3. *Fuchsia fulgens*. Cross sections below ovules and a little above lowermost ovules; longitudinal section through most of two septa and parts of two locules.—4. *Oenothera biennis*, cut a little above lowermost ovules. Longitudinal bundles as well as transseptal bundles supply ovules in Fig. 2, but it is clear from Fig. 3 that these longitudinal bundles are upward extensions of transseptal bundles. Van Tieghem pointed out in a legend that there are no central bundles in the flower's base, and his text (p. 153) called attention to the oddity: "Cette absence de faisceaux longitudinaux dans les bords mêmes des carpelles est une circonstance assez curieuse"



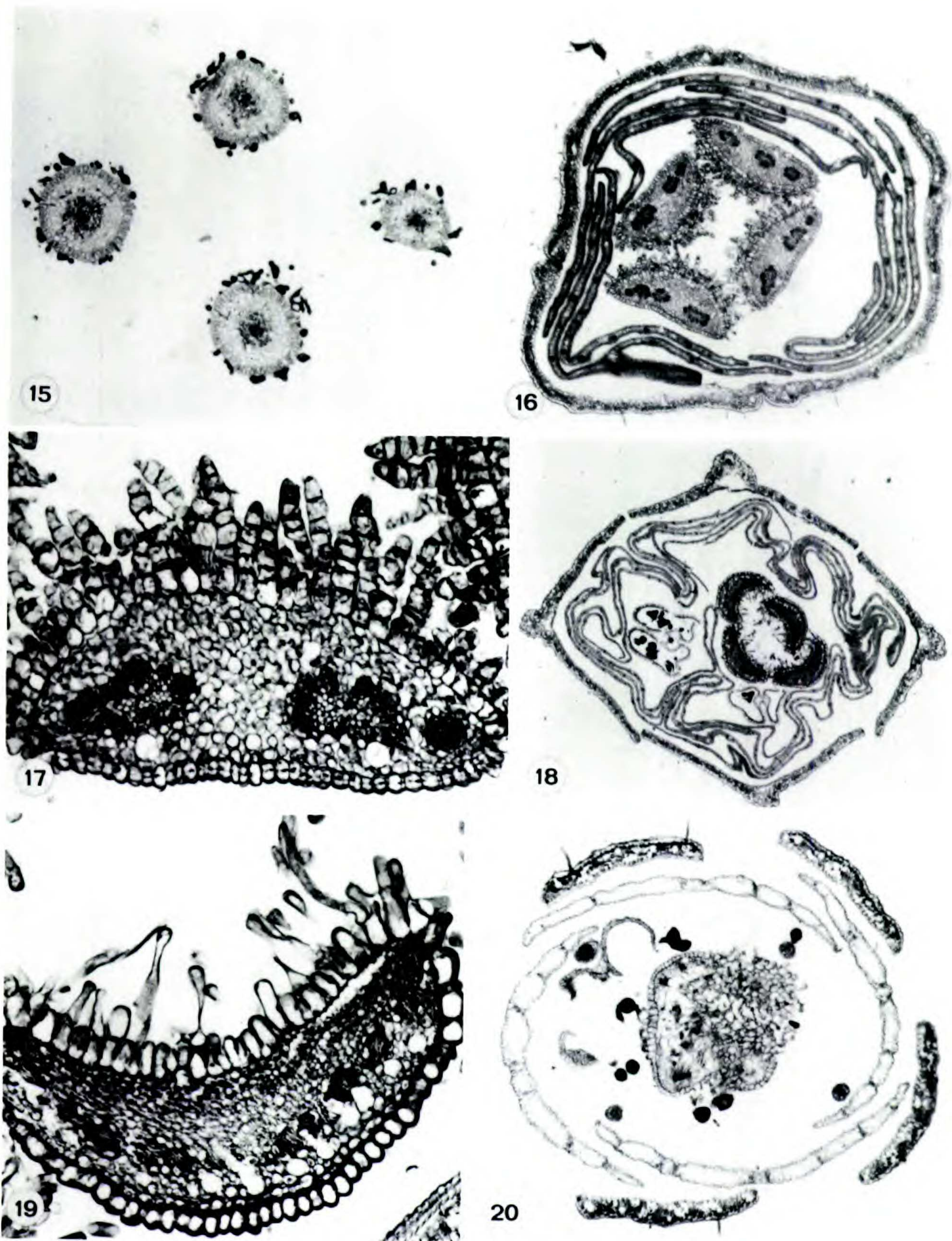
FIGURES 5-10. Diagrammatic longitudinal sections showing androecial nectaries (stippled) in Caryophyllales.—5. *Phytolacca icosandra* (Phytolaccaceae), cut through locule and septum.—6. *Alternanthera sessilis* (Amaranthaceae).—7. *Scleranthus perennis* subsp. *dichotomus* (Caryophyllaceae).—8. *Pereskia diaz-romeroana* (Cactaceae).—9. *Rhipsalis houlettiana* (Cactaceae).—10. *Portulaca grandiflora* (Portulacaceae). All from Zandonella (1972) with permission.



FIGURES 11-14. Gynoecial nectaries (arrows) in members of four families.—11. *Clethra canescens* (Clethraceae).—12. *Rhododendron japonicum* (Ericaceae).—13. *Ehretia navesii* (Boraginaceae).—14. *Eurya japonica* (Theaceae). All from Brown (1938).

enlarge the nectary without moving it, giving it the pulvinate or toroidal form we see in many kinds of flowers. Or such selection could cause the nectary to extend further up one side of the junction or the other. Once the nectary had shifted to one side, it would not easily move back across the notch and up the other side.

To apply this line of thought to the Onagraceae, one must begin before the ovary was inferior, with an ancestral group in which some members had nectaries at the junction, some to one side of the junction, and some to the other, the same sort of diversity in nectary placement still found in the neighboring family Lythraceae. *Ludwigia* evolved from members with nectaries more to the gynoecial side and got the inferior ovary independently of the other onagrads. Transseptal bundles evolved with the inferior ovary in both the *Ludwigia* line and the main line. (They are found here and there among other myrtalean families, too, but only where the flowers are hypogynous.) The gynoecium's old central bundles vanished from the main line, transseptal bundles replacing them completely. In the *Ludwigia* line, however, the central bundles stayed on as the transseptal



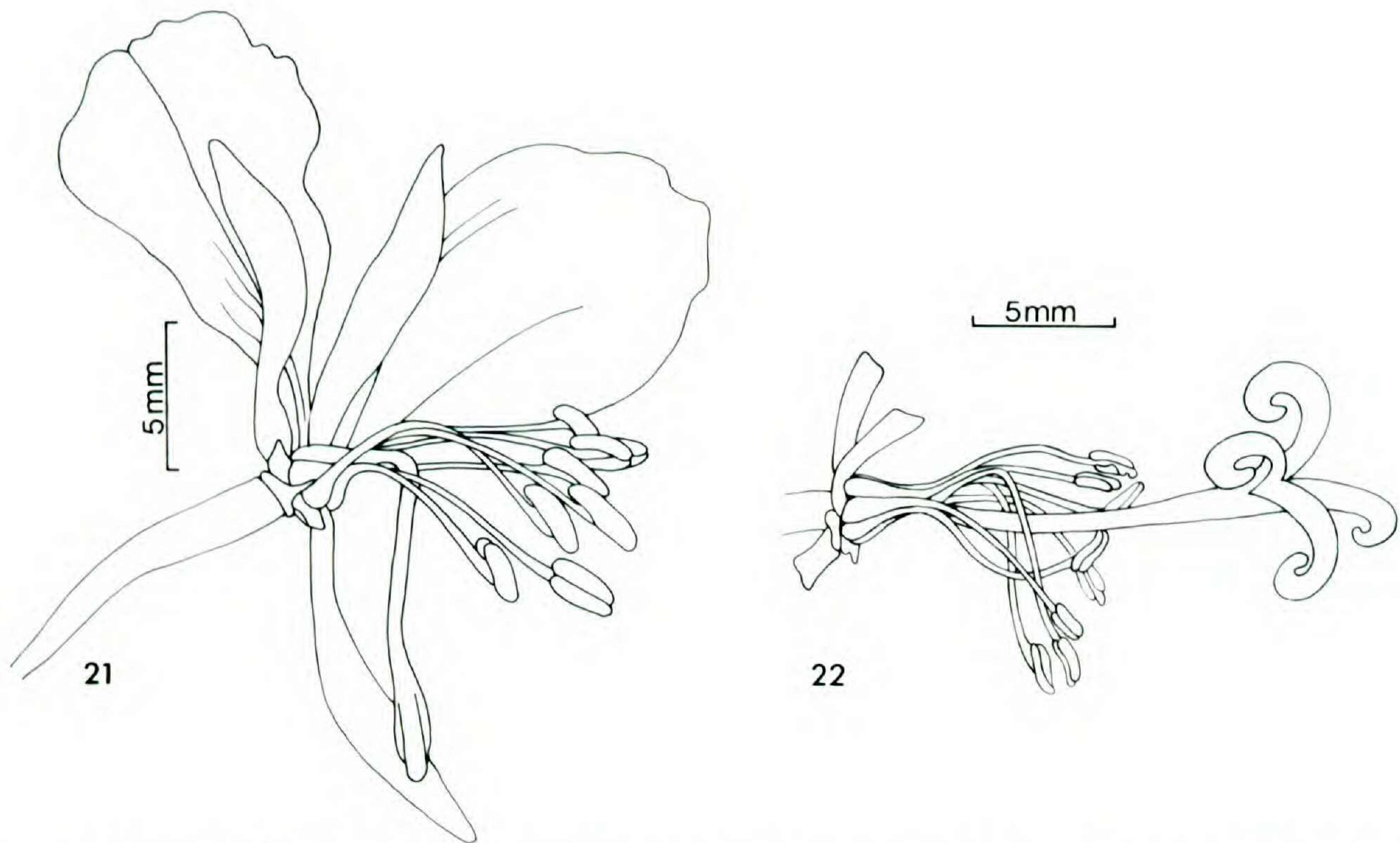
FIGURES 15-20.—15. *Oenothera rosea*, Raven 19084 (DS). Cross section through four stamens showing circular outlines, all-around receptivity. $\times 27$.—16. *Epilobium hirsutum*, cultivated, Missouri Botanical Garden. Cross-section through stamens showing flatter outline. $\times 28$.—17. Same, one stigma enlarged. Note receptive inner surface modified by cell divisions. $\times 170$.—18. *Clarkia imbricata*, cultivated, University of California, Berkeley. Cross section through stamens. $\times 11$.—19. Same, one stigma enlarged. Receptive surface has undergone fewer divisions than that of *Epilobium*. $\times 80$.—20. *E. minutum*, cultivated, Missouri Botanical Garden (seeds from Seavey in 1974). Section shows pollen germinating on stigma before anthesis. Stigma obscurely lobed in carinal radii. $\times 47$.

supply evolved. Here the double-barreled vascular system tied in adaptively with hypogyny and big placentas: 2-way transport within the inferior ovary sustained more ovules and raised the reproductive rate (Eyde, 1981). *Ludwigia*'s divergence from the main line onagrads was furthered by its early entry into wet but unstable sites where populations that could colonize quickly had a marked competitive edge. Evidence for this can be seen in the wet habitats of today's ludwigias (Ramamoorthy, 1981) and in the widespread occurrence of *Ludwigia*-like pollen in swamp deposits of early Tertiary epochs (references in Eyde & Morgan, 1973; see also Muller, 1981).

Comparisons within the Onagraceae and with selected members of other myrtalean families (Eyde, 1977, 1981) indicate that flowers of ancestral onagrads were isomerous and diplostemonous and had more than four appendages in each whorl. Deeply cleft placentas bore more or less 2-seriate ovules as in *Hauya* and some fuchsias. Around the superior gynoecium was a floral cup that varied in prominence from species to species. Members of the *Ludwigia* line need never have been pollinated by anything but the same sorts of unspecialized insects now pollinating them. Main line onagrads, on the other hand, coevolved with long-tongued insects, and a floral tube was part of the evolutionary package. For the mainliners, the evolution of the inferior ovary may have been just one aspect of an overall reshaping of the flower toward efficient and restricted use by more and more specialized pollinators.

An anatomist must savor the systematic insights gotten from *Ludwigia* flowers because the floral structure of other onagrads is not so instructive. Lately, I have been looking at the commissural stigmas found nowhere in the family but in *Clarkia* and in the Epilobieae—*Epilobium* and *Boisduvalia*. Wherever there are four stigmas (for present purposes the distinction between four stigmas and four stigmatic lobes is one of degree only) in these genera, they are in line with the sepals and the gynoecial septa, not with the petals and locules as is true of other onagrads with cruciform stigmas. This difference is easily overlooked because styles rotate a bit in the bud, but other differences go with the positional differences. *Oenothera* stigmas, for example, are circular in cross section; each has but one big vascular bundle and a smooth epidermis that is receptive all around (Fig. 15). *Epilobium*'s commissural stigmas are flatter structures (Fig. 16), with the upper epidermis modified by division and radial elongation of its cells (Fig. 17). Here the vascular supply consists of plural bundles connecting below with the four main style bundles (Bonner, 1948, fig. 12), which are in the petal radii. The South American endemic *Boisduvalia subulata*, the only boisduvalia with expanded stigmas, has stigmas like those of *Epilobium*; so does *Clarkia* (Figs. 18–19) except that the epidermal cells of a *Clarkia* stigma lengthen irregularly and divide infrequently.

The three genera are constant for the trait in that the stigmas never expand much in the normal (carinal) radii; in general, the style of an outcrosser ends in four commissural stigmas (Figs. 21–22) and that of a self-pollinating species ends in a small, more or less capitate or discoid stigma (Fig. 20). I say more or less because the stigmas of selfers can show lobing in cross-section, but the lobes are so shallow and so variable as to be useless to a taxonomist. I sectioned stigmas from four collections of *Epilobium paniculatum* (pickled material, 2–4 flowers

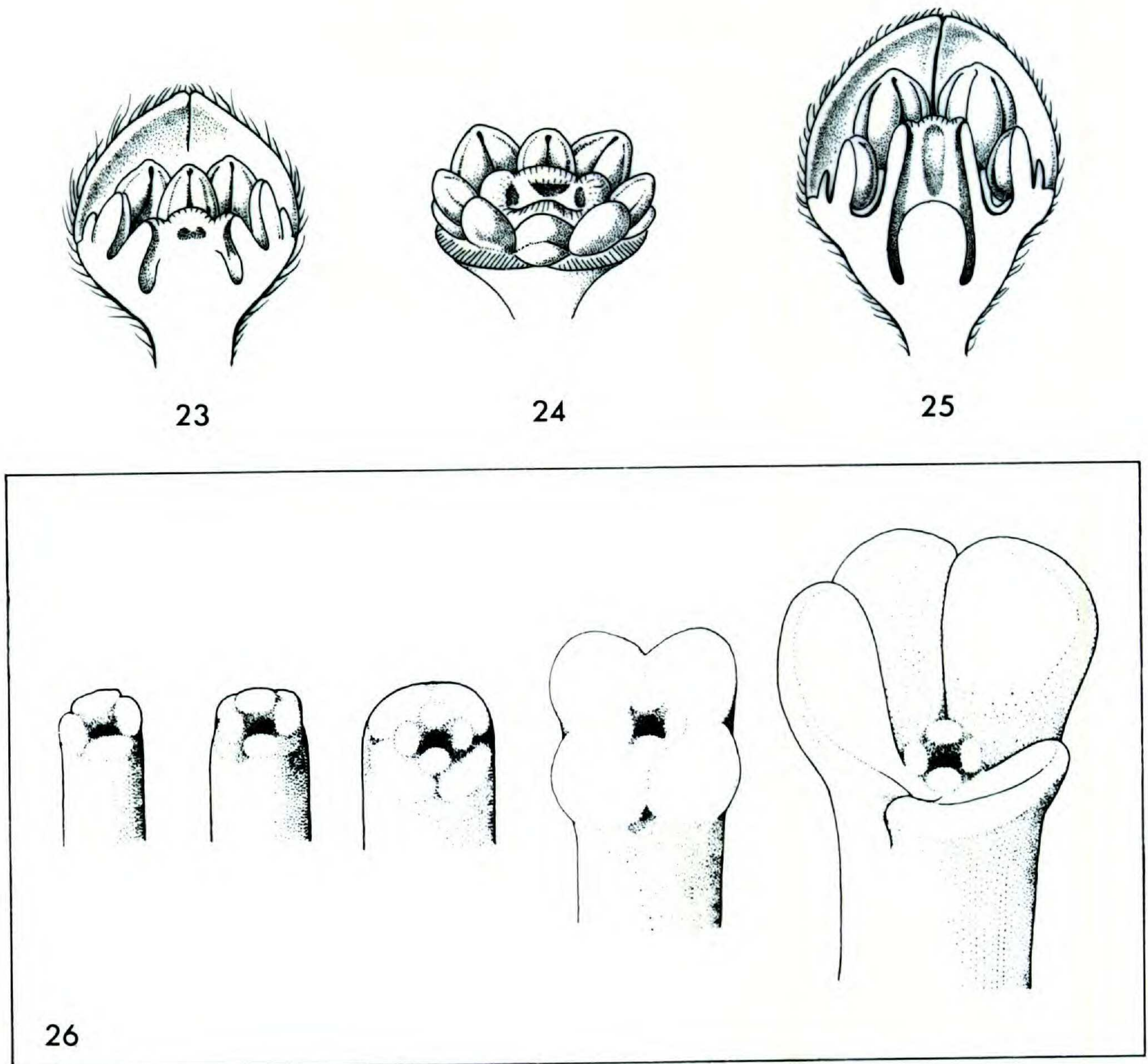


FIGURES 21–22. Protandry in *Epilobium angustifolium*, redrawn from Kartashova (1965).—21. Flower at pollen-shedding stage.—22. Later stage, commissural stigmas receptive to cross-pollination, largely by bees. Barcianu reported the odd disposition of *Epilobium*'s stigmas in 1874, but the observation went unheeded by systematists.

each), and this is what I found: no lobes in *Raven 23000* (DS); slight carinal lobes in *Raven 26465* (MO); slight commissural lobes in two plants cultivated at the Missouri Botanical Garden, one sent to me as *M554*, the other as “seeds from *Seavey 1128*.”

Unfair as it may seem to a systematic anatomist, commissural stigmas are a parallel development in *Clarkia* and *Epilobium*, a structural aspect of protandry rather than a mark of shared ancestry, for the genera are far apart on other evidence. Those epilobiums and clarkias that have changed—reverted, I think—from protandry to selfing, have done away with commissural stigmas as part of the change. And if Raven (1979: 591) was right in saying the South American endemic *Boisduvalia subulata* began to outbreed after its forebears arrived in South America, it, too, got its commissural stigmas independently. Commissural stigmas form late in floral ontogeny between the tips of the four gynoecial primordia, tips that would in *Oenothera* lengthen into carinal stigmas. They overtop the primordial tips as the style grows (Kowalewicz, 1956; Mayr, 1969; Figs. 23–27). No doubt this is a reason for the plasticity of commissural stigmas. Arising when the flower bud is fairly well developed, they can be gained or lost without disrupting other developmental events.

Boisduvalia subulata is the only boisduvalia with clearly and constantly divided stigmas. Other boisduvalias have more or less capitate stigmas. The same was true, I think, of the ancestral group common to *Boisduvalia* and *Epilobium*, because a more or less capitate ancestral stigma links the Epilobieae straight-away with the other onagrads: Raven's (1977: 330) 4-lobed ancestors are not needed for the tribe as a whole and would require still earlier ancestors with



FIGURES 23-26. Ontogeny of stigmas in *Epilobium*.—23-25. *E. angustifolium*. Two early stages in floral development, redrawn from Payer (1857). 23 & 24 show same stage; bud is halved in 23, dissected in 24. 25 is later stage. Note gynoecial primordia in carinal radii.—26. *E. hirsutum*. Mayr (1969) drew this sequence of hand lens views showing commissural overtopping of the primordia. Reproduced with permission.

clavate or capitate stigmas to tie the *Epilobieae* to the rest of the family. The evolutionary history that Raven infers for *Boisduvalia subulata* can serve as a model for the tribe's history except that the scene shifts to North America. I picture the tribal ancestors as a small population; largely self-pollinating but able to outcross; perennial and xerophytic like the more archaic *epilobiums* but closer to *Boisduvalia* in their floral structure, their coma-free seeds, and their chromosome numbers (here I follow Raven, 1977). Within this population and its descendants enough outbreeding, isolation, and selection took place for *Boisduvalia* to diverge and radiate into the moister habitats that all six species now occupy. Radiation was faster and more effective in the *Epilobium* line because comatose seeds, commissural stigmas, and protandry evolved early and because commissural stigmas remitted rather readily whenever changed conditions fa-

vored modal selfing. In short, I picture the tribe's evolutionary history as more punctuated than gradual and the capitate stigma as a kind of punctuation mark.

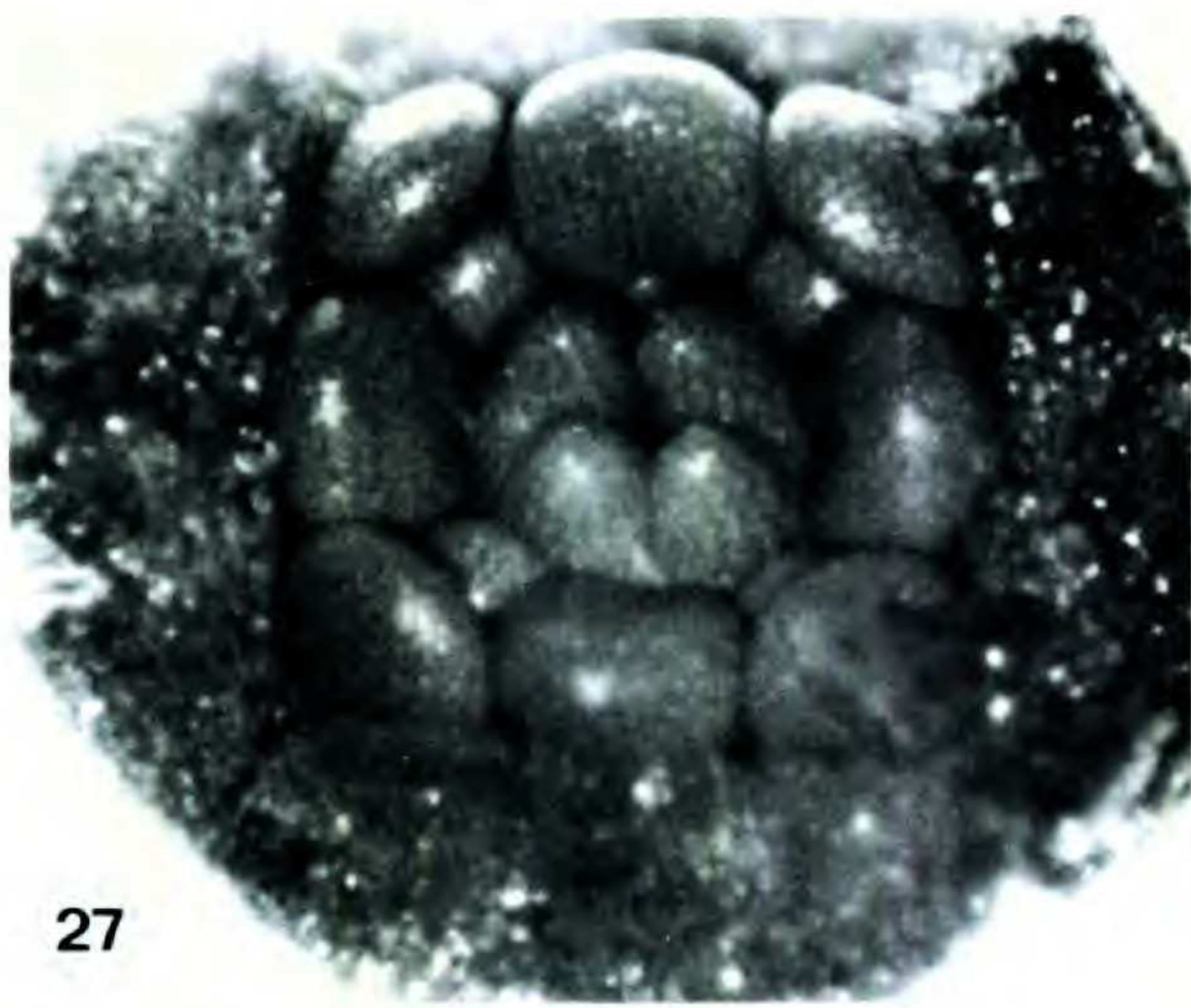
Clarkia's history was similar but even more punctuated. Indeed, the genus holds the best based botanical examples of sudden speciation (see Raven & Axelrod, 1978: 82–83; Stanley, 1979: 168, 175). The kinship of *Clarkia* to its nearest neighbor, the monotypic genus *Heterogaura*,³ differs from the *Epilobium-Boisduvalia* kinship in that there is no need to infer remote common ancestry: the forebears of *Heterogaura* would fit well in *Clarkia*. *Heterogaura* is self-pollinating, to be sure, but its shallow commissural lobes probably came from protandrous precursors.

It is easier to point to a connection between commissural stigmas and protandry than to say how the two are linked. I suspect it is through auxin-induced lengthening of the style, the auxin source being the anthers (see Weinland, 1941, for experimental evidence of this in *Oenothera*). If this is true, there ought to be a consistent timing or structural difference between the androecia of "commissural" species and those of their "capitate" relatives, and I have scanned sectioned flower buds for such differences, but so far without success.

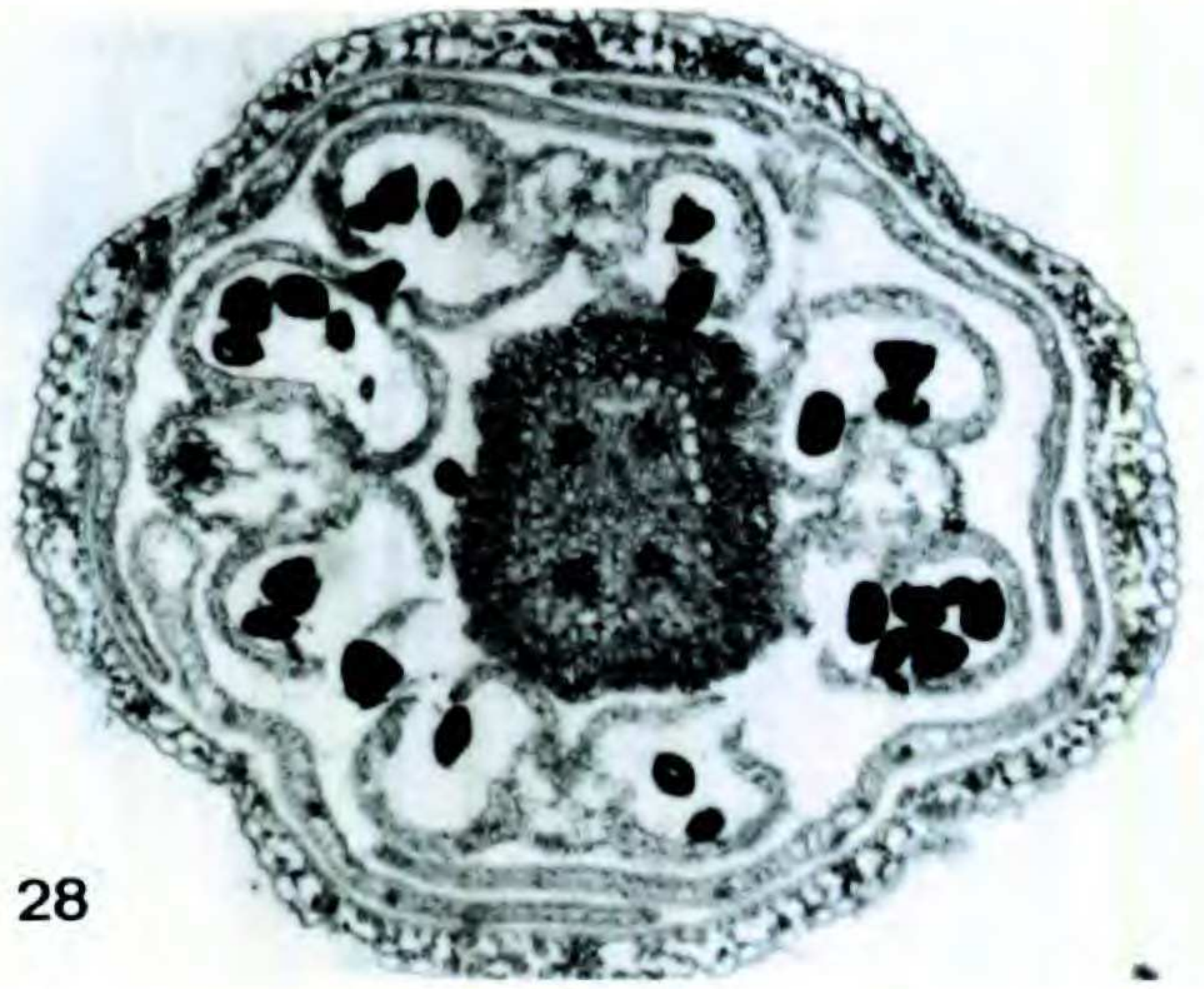
Although the commissural stigmas discussed here are disappointing in that they do not mark a single alliance within the Onagraceae, they do add to our general understanding of the peculiarity. Clearly, Eames's (1961: 244) explanation of commissural stigmas, that they are "the result of the fusion of the lobes of a divided stigma with those of the adjacent carpels," will not work for this family. And it would be interesting to know whether commissural stigmas arose in any other families at abrupt evolutionary turning points, self-pollination going over to outbreeding, as seems to have happened in the Onagraceae.

The gynoecial vascular system of *Gayophytum* is another onagraceous novelty that may aid our overall understanding of floral evolution. All nine species (Lewis & Szweykowski, 1964) have 2-locular gynoecia, but the vascular system is that of a 4-merous gynoecium. Four bundles run through the petal radii of the style and end distally in a globose to hemispherical stigma (Fig. 28). Followed downward into the neck between the inferior ovary and the superior part of the flower (Figs. 29–31), each of the four bundles merges with a bundle leading to a petal and an antepetalous stamen. It is easy to track the four bundles on downward from the neck because the path of each is marked by a narrowing of the ovary wall: in cross sections there is an internal notch and an external notch at each of the four positions (Fig. 32). These bundles are more tenuous than the bundles alternating with them, that is, than the four strands supplying sepals and antepetalous stamens. They are so tenuous, in fact, that I question whether they carry much water and photosynthate. It is clear, however, that they have another

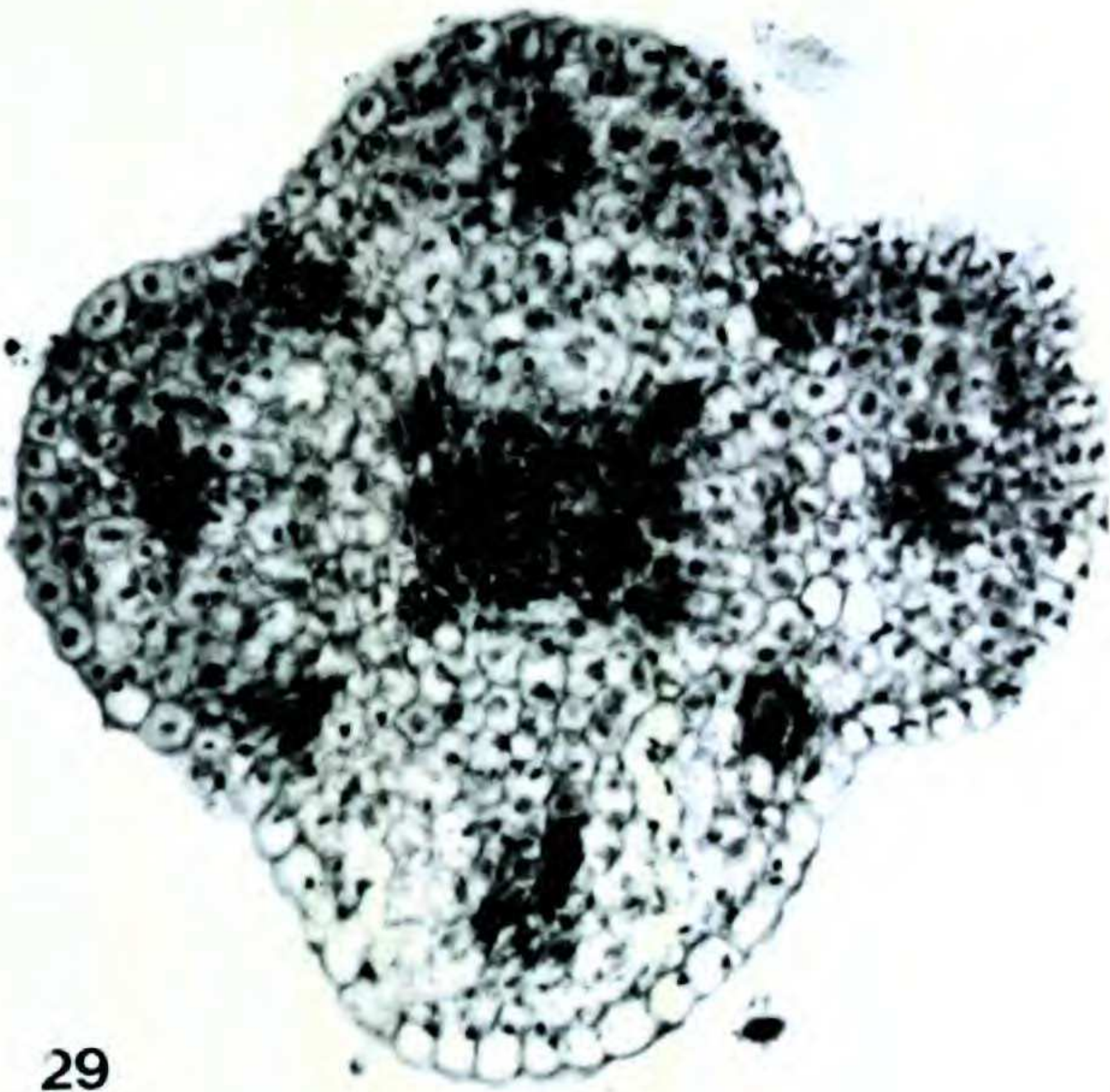
³ Incongruously, since research on *Clarkia* has gotten to the electrophoretic analysis of genes, simple observations yield new information about *Heterogaura*. I looked at nine serially sectioned flowers from two wet collections—*H. Lewis 1628* (LA), *Gottlieb in 1977* (MO)—and found *Heterogaura*'s gynoecium to be zygomorphic and 2-merous. The ovarian septum is in the median plane, but the two locules lie more to the abaxial side of the flower than to the adaxial, suggesting the phyletic loss of a matching pair of locules from the abaxial side. Sectioned styles show two vascular bundles displaced toward the abaxial side, and the stigma has two shallow, unequal lobes centered in the median (commissural) plane.



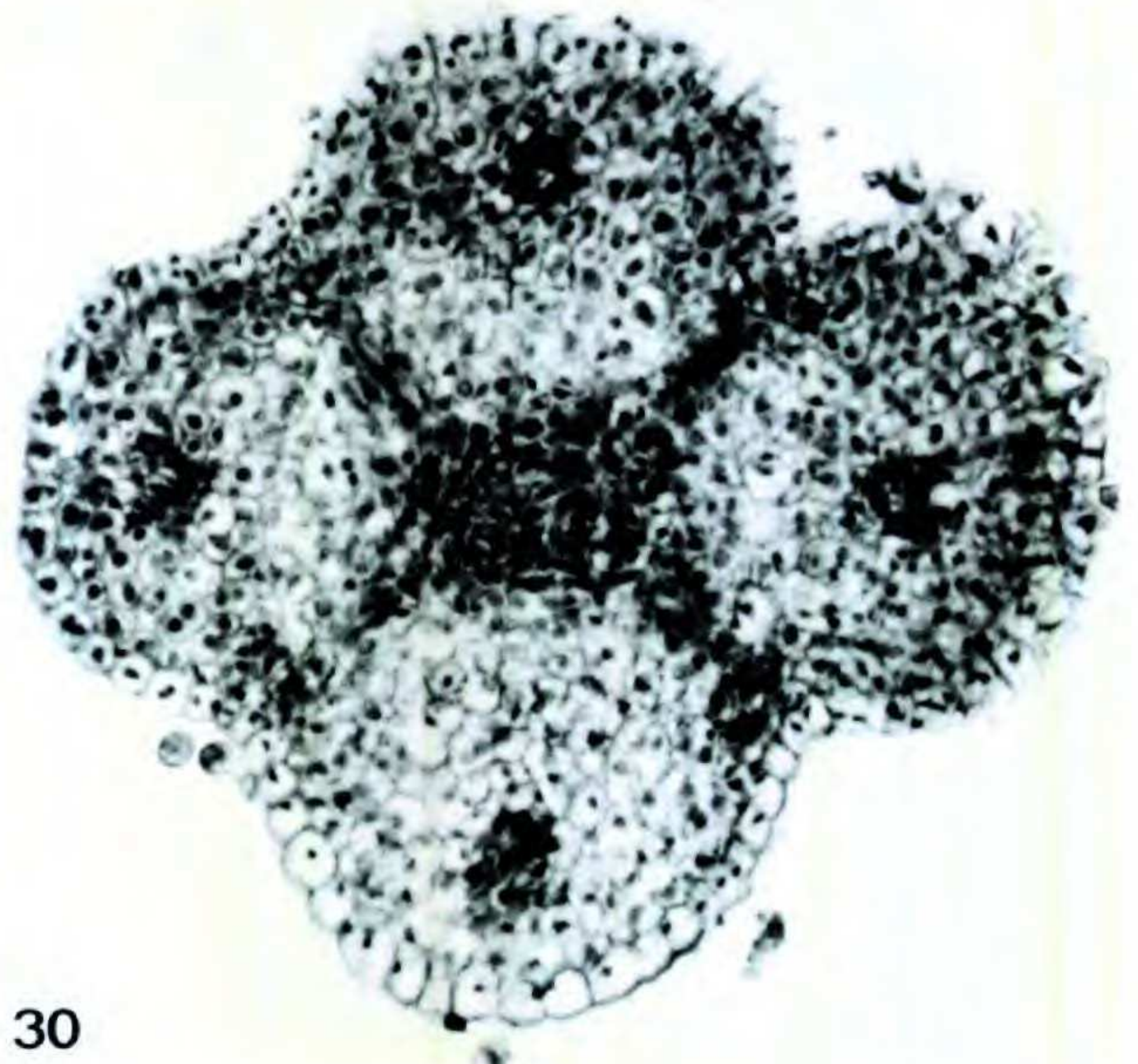
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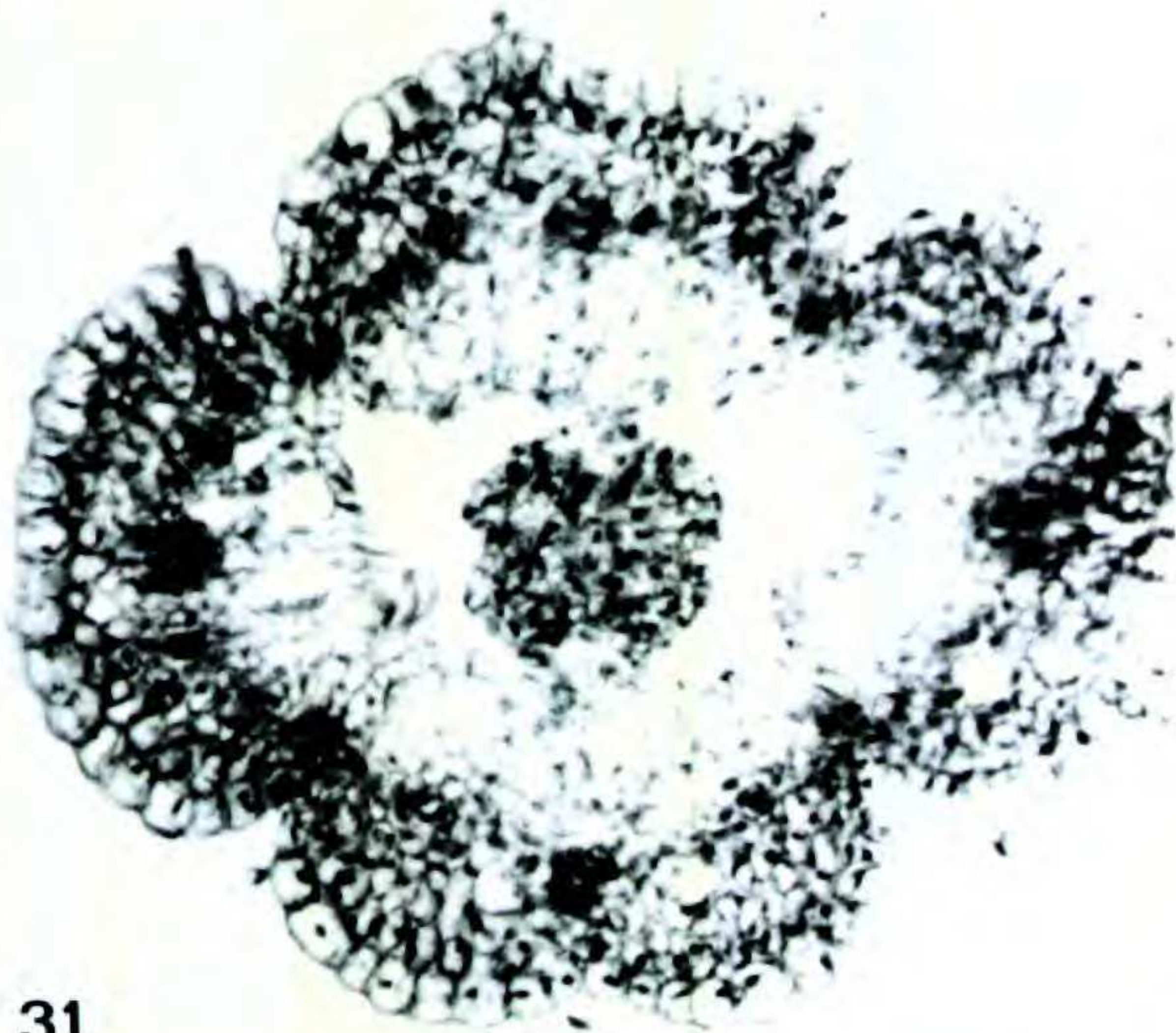
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FIGURES 27-32.—27. Dissected flower bud of garden fuchsia showing four gynoecial primordia at center. Primordia like these become carinal stigmas or receptive lobes in most onagrads but are overtopped by commissural stigmas in protandrous clarkias and epilobiums: see Figs. 23-26. Incident light photo courtesy of R. Sattler (Sattler, 1973: 117). $\times 85$.—28-32. Gynoecial vasculature of *Gayophytum* in cross-section.—28. *G. racemosum*, Raven 26420 (MO), cut through stigma to show four bundles aligned with petals. $\times 54$.—29-31. Same collection. Sections from a second flower follow four style bundles basad through epigynous neck to their junction with bundles supplying petals and antepetalous stamens. 29 & 30, $\times 150$, are adjoining sections. 31, $\times 120$, is about $60 \mu\text{m}$ below 30.—32. *G. diffusum*, Seavey 1096. Four dehiscence lines (darts) in 2-locular ovary are downward extensions of style bundles. Arrows mark sites that the vascular anatomist of yesteryear would call sterile placentas. $\times 85$.

function. Tenuous as they are, these bundles establish weak lines in the ovary wall along which the mature capsule splits. Natural selection has retained them not because of their role in transport but because the freeing and scattering of seeds would go awry without them. With the evolutionary loss of the lateral septa and the evolutionary flattening of the capsule, these four "dehiscence" bundles shifted somewhat toward the transverse plane, further obscuring their origin, in Eamesian terms, as carpel midveins.

As far as I know, *Gayophytum*'s gynoecial vasculature is something new to the literature of floral anatomy, the nearest approximation being in one or another of the pseudomonomerous gynoecia figured by Eckardt (1937; see especially Abb. 25). At first glance, cross sections of a *Gayophytum* ovary bring to mind the crucifer gynoecium, subject of so many wrangles among morphologists. Looked at more closely, the *Gayophytum* gynoecium is quite unlike a real crucifer gynoecium or any morphologist's diagrammatic version of a crucifer gynoecium. A formal, Eamesian interpretation of *Gayophytum* would delineate four carpels, their midveins (darts in Fig. 30) placed diagonally with respect to the pedicel and bract. There would be sterile placentas in the transverse plane (arrows in Fig. 30), but no solid carpels anywhere. In contrast, Eames's interpretation of the crucifer gynoecium (Eames & Wilson, 1930; Eames, 1961) put carpel midveins in the median and transverse planes: those in the median plane belong, he said, to solid carpels. In Eames's view a dehiscing crucifer carpel splits where the solid carpels join the other pair, not along the midveins as in *Gayophytum*. Although Saunders's (1923, 1937–1939) ideas on gynoecial evolution were far from Eames's, her arrangement of crucifer carpels was the same. Indeed, anyone trying to diagram crucifer carpels in another position would come a cropper on *Rorippa bareifolia* (Stuckey, 1972: 380), a species with four fertile locules, two centered in the median plane and two in the transverse plane. I could go on to give my own interpretation of the crucifer gynoecium—the only good and true one, of course—but we are here to talk about the Onagraceae, and my revelations on that family are enough for one symposium.

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